

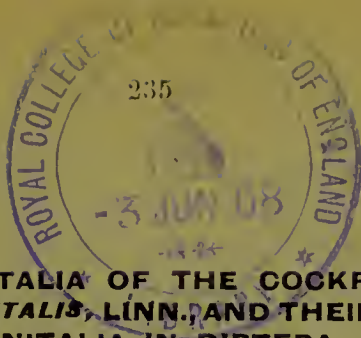
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REPRINTED
FROM THE
JOURNAL OF THE
QUEKETT MICROSCOPICAL CLUB.

20, HANOVER SQUARE, LONDON, W.

APRIL, 1908.





THE MALE GENITALIA OF THE COCKROACH, *PERIPLANETA ORIENTALIS*, LINN., AND THEIR HOMOLOGY WITH THE GENITALIA IN DIPTERA.

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(Read January 17th, 1908.)

PLATES 19 AND 20.

THE sexual armature of the male of *Periplaneta* has every part present (or its homologue) that is found in the most elaborate combination in the Muscidae, but it is extraordinarily difficult to understand and homologise, as every piece is asymmetrical. In many species of the Orthoptera, fertilisation is brought about by the male transferring a spermatophore to the cloaca of the female; Dr. Benjamin Lowne thinks that this is most probably the method by which the cockroach is impregnated.* Certainly there are no signs of an ejaculatory duct in the penis, though the other parts are highly organised, and it can be seen that the elaborate apparatus found in other insects for storing and controlling the flow of spermatozoa, is represented by an equally, or even more elaborate apparatus for storing and protecting the spermatophore. Bearing in mind the great probability of Dr. Lowne's suggestion, not only as coming from so high an authority on insect anatomy, but supported by the details of the structure, we may conjecture that the genitalia of this order of insects are not (unlike the mouth parts) of archaic type, but are a specialisation, which has resulted in the complete transformation of the mechanism of the whole organ, and of the functions of its parts, the ejaculatory duct changing its course and opening in the centre under the part which I call the cover (Pl. 20, Fig. 6), while a special gland is present, opening between the paraphalli, which has functions probably connected with the formation of the spermatophore. I shall show later that the palpi usually present

* *The Anatomy, Physiology, etc., of the Blow-fly*, p. 664 (1895).

in the interior of the genitalia are aborted, but there are a number of sensory hairs which indicate the site of the left palpus, while the right has completely disappeared. This remnant indicates by its presence that in some period of the evolution the palpi were fully developed, and that changes have taken place. The functional changes undergone by these parts are, very possibly, the cause of their extraordinary asymmetry; similar conditions are found in *Periplaneta americana*, Linn., and a species of *Mantis* as shown in the descriptions of Mons. A. Peytoureau.*

The exterior parts are less difficult to recognise, as they are symmetrical, but they are very dissimilar from their homologues in other insects, and quite archaic in type, as may be seen by a comparison with the Crustacean Oniscidae (wood-lice).

I shall now describe each portion of the armature separately, with the nomenclature that has been formulated for the corresponding parts in Diptera†; though this is an inversion of the usual process, yet, as I have endeavoured to show, it is advisable, owing to the exigencies of the case.

(a) *Forcipes inferiores*.—These are represented by a symmetrical pair of simple unsegmented rods with blunt points, inserted in sockets and placed laterally on the ventral side of the abdomen (Fig. 5).

(b) *Forcipes superiores*.—These I homologise with the cerci; a symmetrical pair of palpi-like organs with sixteen joints and moderate pubescence, which is more marked on one side than on the other. Some delicate sense-hairs can be seen scattered among the more robust tactile-hairs. One of my preparations exhibits a complicated series of nerves and ganglia, showing that the part fulfils sensory functions, as these organs often do in the Diptera (Fig. 4).

(c) *Lamina superior*.—A highly chitinised plate which covers the bases of the *forcipes superiores* corresponds with this.

* *Morphologie de l'armure génital des insectes*, A. Peytoureau. Paris, 1895.

† The Genitalia of both Sexes in Diptera. W. Wesché, *Trans. Linn. Soc. London*, 2nd. Ser. Zool. vol. ix., Part 10, 1906.

(d) *The extremity of the penis.*—In most insects this part is membranous, and is pierced by the orifice of the ejaculatory duct. Here there is no duct, and its usual place is closed by a membrane covered with very short cilia, forming a fur or delicate tomentum; where this cover ceases, the membrane is more chitinous, and has a marking of minute scale-like sculpturing of the chitin, 140 to the mm. The whole part fits into the theca (Figs. 1, 2, d).

(e) *The theca or penis sheath.*—This part in the flies does not reach to the end of the ejaculatory duct, and it not only forms a support to the *hypophallus*, but also to the appendages which surround it—the *spinus*, the *palpi*, and the *forcipes interiores*. In *Periplaneta*, however, it supports the *hypophallus* and the *spinus*; it is separated from the platforms from which spring the *forcipes*, and its extremity is elongated into a cowl-like head, covering the membrane of the ejaculatory duct (Figs. 1, 2, e).

(f) *The paraphalli.*—There are two asymmetric rods with pointed ends which are in similar positions to these organs in the Muscidae. They are the “saddle-shaped piece” of Professor Miall, and between the forks is the opening of his “conglobate gland.”* The paraphallus on the left of the penis is furcate, and has a minute roughening of its surface, similar to that found on the membrane at the extremity of the penis (Fig. 3).

(g) *The hypophallus.*—This is represented by a thoroughly characteristic piece, highly chitinated and covered with aculeations. It is a plate, bent round so as to nearly form a tube, and it is connected with the theca by hyaline membranes. The structure is quite similar to that found in Lowne’s “bulb” and “hypophallus” in the Blow-fly (Fig. 2 g).

(h) *Spinus titillatorius.*—This organ in *Periplaneta* has been regarded as the type, and from it is derived the name as applied to other insects. Being the single unpaired organ, it is the key to the homology. It is a long, highly chitinated tube, with a transverse arm at the extremity, the arm having a small aculeation on the underside. At its base is a piece which seems

* *The Cockroach*, Miall & Denny, p. 174, 1886.

to be an articulation (Figs. 1, 2, v, and 7). Membranes connect the *spinus* with the *theca* and *hypophallus*, and enclose this piece (Figs. 1, 2, h).

If we indulge our imagination, we can form a mental image of some annulated, worm-like creature, low in organisation, scarcely, if at all, higher than a colony of polyps; each annulation complete in itself, with alimentary canal, genital pore, and some form of rudimentary appendages. The genital pore, as we have found in the majority of creatures, would be on the side opposite the oral aperture. That being so, at one end of this compound worm would be a mouth and at the other a pore. These, from their favourable situations, monopolised the work, and the others atrophying from disuse, or, if part of the alimentary canal, joining on to the mouth of the next segment, evolved into a worm which was compound only in the number of its appendages and annulations, and would be rather lower in the scale of life than *Peripatus*. From this we can see why the ovaries and testes of insects are always found at the posterior end. It also explains in some measure the anomalous genitalia of the male dragon-fly (Odonata).

To continue our phantasy, in the course of ages, one or more sets of the appendages were used at both extremities, either to grasp food or to hold a partner in coitus. Slowly and by degrees modifications in the appendages, which were of advantage to the parent, were transmitted to the offspring and became established, until finally the appendages of a number of segments were brought into use and were changed into hooks, blades, and feeling-organs, grouped round the mouth at one end and the pore at the other. A fold of skin in the median line was also modified, either into a hook or a protection of the important apertures. These folds are now represented by the single unpaired organs which are found both in the mouth and the genitalia. In the former it is the *lingua*, in the latter the *spinus titillatorius*. Such is the theory which has been put forward to explain how the com-

plications at the extremities of an insect have been produced by gradual changes in the more simple appendages.

(i) *Forcipes interiores*.—These are represented by two unsymmetrical pieces, the one on the left having the point twisted round like a corkscrew, the other furcate; their upper ends connect by means of a hyaline membrane, while their bases join with a complicated structure, consisting of a number of plates and membranes, with extremely elaborate muscular attachments, which form the containing apparatus of the spermatophore. This portion of the containing apparatus seems homologous with that part of the theca which in the Muscidae supports the *titillator*, *forcipes interiores*, and the *palpi genitalium*. This view is strengthened by the situation of the remnant of the palpus.

(k) *Palpi genitalium*.—The organs are aborted, but the site is marked on the left side, on a piece which is soldered to the left forceps, by a number of sensory hairs. Comparing it with remnants of palpi in other parts and in other insects, I have no hesitation in identifying this. The absence of a similar vestige on the right side is accounted for by the situation of the "cover" (Fig. 6), which would quite shut off this side from any function.

(m) *The great apodemes*.—I have found on each side of the theca two small islands of chitin, surrounded by a sea of hyaline membrane. They appear to be without any function, and are nearly suboval plates tapering to points. From their structure and from their position, I consider these as the atrophied remains of the apodemes, whose function is so important and whose presence is so constant in most insects. Their disuse has been brought about by the changes already discussed (Figs. 1, 2, m).

(o) *Sacculus ejaculatorius*.—This organ in the Muscidae is membranous, but in the Tipulidae it has a chitinous structure, and suggests that it has its counterpart in the very complicated

series of pieces which form the containing apparatus; besides the part at the base of the left forceps which carries the remnant of the palpus, and which is homologised as part of the theca, there is a convoluted plate below (Fig. 9), a cover which is very prominent on the right side (Fig. 6), a plate which forms an upper part (Fig. 12), and a dome-shaped piece (Fig. 11) which contains an articulation to the convoluted plate (Fig. 13). These parts form connections to those attached to the forceps; they do not readily separate when dissected out, and are apt to break and consequently difficult to study.

The convolute plate has some part of the surface roughened with minute scale markings; a similar structure has been noted on the left *paraphallus* and on the part that represents the orifice of the penis. This suggests itself to me as a surface to which a semi-viscid body would cling, yet not stick, probably regions of contact with the spermatophore.

(p) *Ejaculatory apodeme*.—This is a shield-shaped piece with a strong chitinous process running down the middle for the attachment of muscles; it is situated in the centre, and appears to work the cover. From its structure and situation I feel fairly sure of the homology of this part, and it is consequently a useful guide (Fig. 10).

Interior organs.—These are comparatively simple, and are amply explained in Professor Miall's and Mr. Denny's excellent monograph (already quoted), and in the late Professor Huxley's work on the Invertebrata,* to which I refer those who wish to study these parts.

Conclusion.—It remains to say that regarding the whole organ as a piece of mechanism, it may be divided into four parts; (1) a tube for the passage of spermatozoa into the containing apparatus, and a gland (Prof. Miall's conglobate) for the production of some semi-viscid fluid, used in the formation of the spermatophore; (2) the combination of the theca and hypophallus, penis, and paraphallus, bending over to place the orifice of the

* *The Anatomy of the Invertebrated Animals*, T. II. Huxley, 1877.



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conglobate gland in contact with the containing apparatus, so mixing the secretion from the gland and the spermatozoa, and forming a spermatophore. This necessary movement of the theca has led to its detachment from its surroundings, already discussed in section (e). (3) The containing apparatus with the covering plate held down over it by the apodeme. On excitement the lever would relax the muscles holding down the cover, and (4) the spinus bending over would transfix a spermatophore, and transfer it to the cloaca of the female. Dr. Lowne quotes Cornelius,* "who gives a description of the sexual act in this insect, and describes it as being accomplished with great rapidity." A fact quite consistent with the explanation of the mechanism offered above.

EXPLANATION OF PLATES 19 AND 20.

The size of the drawings on Plate 20 has been regulated by convenience. Their true relative magnitudes are shown on Plate 19.

The following letters are used in the plates :

- d.* The extremity of the penis.
- e.* Theca.
- f.* Paraphalli.
- g.* Hypophallus.
- h.* Spinus titillatorius.
- i.* Forcipes interiores.
- k.* Palpus genitalium.
- m.* Great apodeme.
- o.* Sacculus ejaculatorius.
- p.* Ejaculatory apodeme.
- r.* Convoluted plate.
- s.* Cover.
- v.* Articulating piece.

Fig. 1. The genitalia removed from the cavity of the abdomen, showing the natural arrangement of the parts, with the muscular structure as seen from the right.

* *Blow-fly*, p. 664.

Fig. 2. The same preparation, seen from the left.

Fig. 3. The paraphalli dissected out from the surrounding parts.

Fig. 4. Forceps superior.

Fig. 5. Forceps inferior.

Fig. 6. Cover of the containing apparatus.

Fig. 7. Articulating piece at the base of the spinus titillatorius.

Fig. 8. The forcipes interiores and the site of the atrophied palpus; (*a*) "corkscrew" forceps, (*b*) furcate forceps, (*c*) site of atrophied palpus, (*d*) portion of containing apparatus—part of theca.

Fig. 9. Convoluted plate, part of containing apparatus.

Fig. 10. Ejaculatory apodeme; in this insect working the containing apparatus.

Fig. 11. Dome-shaped piece (part of containing apparatus); (*a*) articulating piece to convoluted plate.

Fig. 12. Upper piece, containing apparatus.

Fig. 13. Articulating piece from interior of dome-shaped piece, enlarged.



